

Assessing the ecological risk posed by a recently established invasive alien predator: *Harmonia axyridis* as a case study

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Abstract Invasive alien predators are a serious threat to biodiversity worldwide. However, there is no generic method for assessing which local species are most at risk following the invasion of a new predator. The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is an alien in Europe and many other parts of the world where it affects other species of ladybirds through competition for food and intra-guild predation (IGP). Here, we describe a method developed to assess which European ladybird species are most at risk following the invasion of *H. axyridis*. The three components of the risk assessment are: the likelihood that the assessed

native species encounters *H. axyridis* in the field, the hazard of competition for food, and the IGP hazard. Thirty native European ladybird species were assessed through data obtained from field observations, laboratory experiments and literature reviews. The species that are considered most at risk are found on deciduous trees, have immature stages which are highly vulnerable to IGP by *H. axyridis*, and are primarily aphidophagous. These species should be the focus of specific studies and possibly conservation actions. The risk assessment method proposed here could be applied to other alien predators which are considered a threat to native species through competition and predation.

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Introduction

Invasive alien species are recognised as one of the main causes of animal biodiversity loss (Bellard et al. 2016). Associated animal species declines are mainly due to competitive exclusion, predation, and introduction of new diseases (Long 2003; Kenis et al. 2009). In particular, alien predatory insects are known to displace insects and other animals worldwide through competition for resources and predation (Snyder and Evans 2006; Wagner and van Driesche 2010). In most cases, invasive alien insects have been introduced accidentally, either as contaminants or stowaways (Hulme et al. 2008). Nevertheless, predators and parasitoids have also been released intentionally in biological control programmes for pest control and a small proportion of them have had undesirable ecological effects on non-target species through competition for resources, predation or parasitism on native species (Hajek et al. 2016). Pre-release risk assessment protocols have the potential to limit the risk of non-target effects but these risk assessments are not yet carried out systematically in all countries (van Lenteren et al. 2006; Hajek et al. 2016). Other risk and impact assessment protocols exist for alien species beyond biological control introductions, many of which are appropriate for assessing predators (e.g. D'hondt et al. 2015; Kumschick et al. 2015) and some protocols have been developed for specific groups of predators, such as ants (Harris et al. 2005). However, these protocols aim at assessing the risk or impact of specific invasive alien species, taking into account their general impact in the invaded habitat (Kumschick and Richardson 2013). In contrast, there is no generic method to assess which particular native species are most at risk following the invasion of a predator. Such knowledge

is usually lacking despite its obvious potential use for prioritising research and conservation actions in the invaded regions.

An example of an introduced arthropod predator that has had undesirable ecological impacts is the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). This beetle was introduced into North America in 1916 and throughout the 20th century to control aphids and coccids, and became established in the 1980s (Roy et al. 2016). Since then, although successfully regulating pest aphids in a range of crop systems, it has spread and increased in number rapidly across most of North America, where it has become the dominant aphidophagous ladybird (e.g. Colunga-Garcia and Gage 1998; Harmon et al. 2007). *Harmonia axyridis* was commercially available in Europe as a pest-control agent from the late 1980s and feral populations were first observed in Germany in 1999 (Brown et al. 2011). The beetle then rapidly invaded most European countries and many other regions on all continents except Antarctica (Roy et al. 2016).

The threat posed by *H. axyridis* to biodiversity and ecosystem functions in invaded regions may be considerable. Impacts on native species can occur both through direct predation and competition for resources. *Harmonia axyridis* has a broad diet, putting many non-target species at risk from predation. Whilst preferring aphid and coccid prey, *H. axyridis* will also accept the immature stages of many insects, including butterflies and other aphid predators (Koch et al. 2003, 2006; Pell et al. 2008). Intra-guild predation (IGP), i.e. the killing and eating of species eating similar, often limiting, resources (Polis et al. 1989), is widespread amongst aphidophagous insects, and *H. axyridis* is known to attack the immature stages of many ladybird guild members (Ware and Majerus 2008; Ware et al. 2008a; Rondoni et al. 2012a, b; Katsanis et al. 2013). Recent observations have demonstrated that *H. axyridis* also feeds on European ladybirds in the field (Hautier et al. 2011; Thomas et al. 2013; Rondoni et al. 2014; Brown et al. 2015).

Negative effects of *H. axyridis* on native Coccinellidae have already been documented in North America. For example, *H. axyridis* was reported to be displacing *Cycloneda sanguinea* (L.), in Florida citrus orchards (Michaud 2002). Similarly, within four years of its arrival in Michigan, *H. axyridis* had taken over

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the status of *Coleomegilla maculata* (DeGeer) as the dominant aphid predator, and a decrease in populations of three other species of ladybird was reported: *Brachiacantha ursina* (F.), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say) (Colunga-Garcia and Gage 1998). However, in an analysis of a 26-years dataset in the same region, Bahlai et al. (2015) confirmed the long term decline of two species only, *C. maculata* and *Adalia bipunctata* (L.).

In Europe, field studies have been undertaken in several countries to monitor changes in populations of native ladybird species following the arrival of *H. axyridis* (e.g. Eschen et al. 2007; Adriaens et al. 2008; Brown et al. 2011). A first assessment of the impact of *H. axyridis* on native species of ladybird in Belgium, Britain and Switzerland showed that some historically widespread and common species are declining (Roy et al. 2012). For *A. bipunctata* in Belgium, the rate of decline warrants red listing as a vulnerable species (Adriaens et al. 2015). However, ladybird populations are known to fluctuate naturally and, thus, it may take several years before a long-term impact can be ascertained. Also, some species were already in decline before the arrival of *H. axyridis*, suggesting that the invasion acted as an additional stressor on insect populations on top of other factors (Roy et al. 2012). Furthermore, general faunistic studies are able to monitor changes in the most abundant species but less common species are only rarely captured. It is essential that research is rapidly centred on those species that are most at risk and so we carried out a qualitative risk assessment for native ladybird species in Europe to determine those species that are most and least likely to decline following the invasion of *H. axyridis*. The risk was assessed for most “true ladybirds” (sensu Majerus 1994, i.e. sub-families Coccinellinae, Epilachninae and Chilocorinae) occurring in Western Europe.

This study also provides us with the opportunity to develop rapid and relevant methods of qualitative risk assessment for established alien predators. In particular, we hope that our approach may be usefully applied to other arthropod predators that are in the process of invasion and for which conclusive impacts on biodiversity are not yet observed or measurable. Also, for already established alien predators the results of such assessments can inform risk management and prioritisation in uninhabited regions.

Materials and methods

A risk assessment involves identifying and quantifying the hazards, and determining the probabilities that these hazards will materialise. The risk is then the product of a likelihood (probability) and a magnitude of hazard (consequence). In this study, the risk posed by *H. axyridis* on 30 native ladybirds (see list in Table 1) was considered as the product of the likelihood that a given ladybird species encounters *H. axyridis* in the field, and the consequence of this encounter, through competition for food and direct predation. Therefore, the risk assessment was carried out in three steps: (1) likelihood of encounter with *H. axyridis* in the field, (2) competition for food, (3) intra-guild predation.

Likelihood of encounter with *H. axyridis* in the field

The likelihood that a native ladybird species encounters *H. axyridis* in the field was measured using field data in Switzerland, Belgium and Britain. Datasets comprising field observations were used to assess spatial and temporal co-occurrence between native species and *H. axyridis*. Since the data in the three countries had not been collected for this particular purpose, sampling and, subsequently, calculation methods differed among countries.

In Switzerland, extensive surveys for ladybirds carried out from 2006 to 2009 in the North-Western part of the country (Cantons Jura, Basel-Landschaft, Basel-Stadt and Solothurn) were used to calculate an ‘asymmetric habitat overlap index’, defined as ‘the proportion of specimens of a given species collected at the same time and the same site as *H. axyridis*’. The habitat overlap is qualified as “asymmetric” because no ladybird has exactly the same habitat as another and, thus, the proportion of specimens of a species X collected with *H. axyridis* will most likely be different from the proportion of *H. axyridis* collected with species X. Surveys (and site locations) were carried out as described in Eschen et al. (2007) and Zindel (2008). Branches of conifers, broadleaved trees and shrubs were beaten over a tray to collect adult ladybirds. Meadows and grasslands were sampled using a sweep net. Insects collected at the same time on the same group of trees (maximum 50 m distance), the same hedgerow (maximum 50 m long) or the same

Table 1 The 30 native coccinellid species for which the risk was assessed, main habitats, asymmetric habitat overlap index in Switzerland, spatio-temporal co-occurrence index in Belgium and Britain and final score of likelihood of encounter

Species	Main habitats	Index %/N (score)			Final score
		Switzerland	Belgium	Britain	
<i>Adalia bipunctata</i> (L.)	Various	69.8/467 (3)	61.2/1800 (3)	19.6/1609 (3)	3
<i>Adalia decempunctata</i> (L.)	Deciduous trees	53.1/292 (3)	63.8/676 (3)	15.1/631 (3)	3
<i>Anatis ocellata</i> (L.)	Coniferous trees	–	50.8/269 (2)	13.4/67 (2)	2
<i>Anisosticta novemdecimpunctata</i> (L.)	Reed beds	–	49.2/177 (2)	3.3/61 (1)	2
<i>Aphidecta oblitterata</i> (L.)	Coniferous trees	3.4/469 (1)	56.0/538 (2)	5.4/37 (1)	1
<i>Calvia decemguttata</i> (L.)	Deciduous trees and hedgerows	–	67.7/421 (3)	–	3
<i>Calvia quatuordecimguttata</i> (L.)	Deciduous trees	44.9/98 (2)	60.6/839 (3)	9.2/303 (2)	2
<i>Chilocorus bipustulatus</i> (L.)	Heathland and other habitats	8.7/46 (1)	59.4/42 (3)	15.6/32 (3)	2
<i>Chilocorus renipustulatus</i> (Scriba)	Deciduous trees	19.5/41 (1)	33.3/264 (1)	6.5/93 (1)	1
<i>Coccinella hieroglyphica</i> L.	Heathland	–	20.3/100 (1)	–	1
<i>Coccinella magnifica</i> Redtenbacher	Close to nests of <i>Formica</i> ants	–	48.1/44 (2)	–	2
<i>Coccinella quinquepunctata</i> L.	Pioneer low vegetation	–	49.2/308 (2)	–	2
<i>Coccinella septempunctata</i> L.	Various	2.3/88 (1)	53.3/2303 (2)	11.3/1897 (2)	2
<i>Coccinella undecimpunctata</i> L.	Herbaceous plants	–	46.3/140 (2)	12.8/39 (2)	2
<i>Cynegetis impunctata</i> (L.)	Wet grassland	–	44.4/30 (2)	–	2
<i>Coccinula quatuordecimpustulata</i> L.)	Dry grassland	–	48.8/44 (2)	–	2
<i>Exochomus nigromaculatus</i> (Goeze)	Heathland and other habitats	–	40.4/65 (2)	–	2
<i>Exochomus quadripustulatus</i> (L.)	Needled conifers, deciduous trees	23.9/117 (2)	57.3/766 (3)	10.9/567 (2)	2
<i>Halyzia sedecimguttata</i> (L.)	Deciduous trees	31.4/35 (2)	56.5/718 (2)	18.5/390 (3)	2
<i>Harmonia quadripunctata</i> Pontoppidan	Needled conifers	27.8/36 (2)	53.9/371 (2)	13.5/111 (2)	2
<i>Henosepilachna argus</i> (Geoffroy)	Low herbage	–	27.3/122 (1)	–	1
<i>Hippodamia variegata</i> (Goeze)	Reed beds, meadowland	4.2/48 (1)	46.5/158 (2)	4.3/70 (1)	1
<i>Myrrha octodecimguttata</i> (L.)	Coniferous trees	–	45.2/151 (2)	12.1/33 (2)	2
<i>Myzia oblongoguttata</i> (L.)	Coniferous trees	–	39.4/53 (2)	15.0/20 (3)	3
<i>Oenopia conglobata</i> (L.)	Deciduous trees	66.7/21 (3)	75.5/192 (3)	–	3
<i>Platynaspis luteorubra</i> (Goeze)	Association with <i>Lasius niger</i>	–	44.8/20 (2)	–	2
<i>Propylea quatuordecimpunctata</i> (L.)	Various	20.5/242 (1)	52.2/1635 (2)	7.9/974 (1)	1
<i>Psyllobora vigintiduopunctata</i> (L.)	Low vegetation	20.3/64 (1)	55.6/867 (2)	7.7/355 (1)	1
<i>Subcoccinella vigintiquatuorpunctata</i> (L.)	Grassland	0.0/46 (1)	35.8/58 (1)	5.6/337 (1)	1
<i>Tytthaspis sedecimpunctata</i> (L.)	Grassland	0.0/336 (1)	42.4/126 (2)	6.0/336 (1)	1

N are sample sizes: for Switzerland, they represent the number of individuals of native species on which the index has been calculated. For Belgium and Britain, they represent the number of species records on which the index has been calculated (*N* data in Table 3 of Adriaens et al. 2008). Information on the main habitats was obtained from the literature on Coccinellidae (e.g. Adriaens et al. 2008; Majerus 1994; Roy et al. 2011; Hodek et al. 2012)

meadow were considered to co-occur. We used data exclusively obtained from sites where *H. axyridis* was thought to be established, i.e. where either few specimens had been found in the previous year, or high numbers of specimens had been found in the year

of observation, and data were collected at the same site for a maximum of two years. Using data from areas where *H. axyridis* was not yet established could have resulted in false negative co-occurrence while using data from sites where *H. axyridis* had been abundant

for more than two years would have the risk that the displacement of native species had already occurred. For 16 native ladybird species, for which at least 20 specimens were collected, the asymmetric habitat overlap index was measured. A total of 2956 records of adult specimens were included in the analyses.

In Belgium and Britain extensive national surveys were carried out in various habitats providing occurrence data for a larger number of species (adults and, to a lesser extent, larvae) but at lower resolution than in Switzerland (Adriaens et al. 2008; Brown et al. 2011; Roy et al. 2012). In Belgium, an index named “spatio-temporal co-occurrence with *H. axyridis*” was calculated by Adriaens et al. (2008), based on occurrence data from 2004–2006 extracted from the large dataset of the Belgian ladybird working group (Adriaens et al. 2012). It was defined as the number of collection events (for which the following information was available: species observed, number of individuals, development stage, observation date, observer and location) where a given species had been found with *H. axyridis*, at the same date in a 1-km² grid cell, divided by the total number of collection events with this species and any other ladybird species, including *H. axyridis* (n = 2699 collection events and over 10,000 individuals). This index was calculated for all native ladybirds selected for the assessment. All species had over 20 records in the database.

The British data were analysed similarly to the Belgian data. Ladybird species spatio-temporal co-occurrence data (i.e. where two or more species were recorded at a site on the same date, whether or not one of them was *H. axyridis*) from 2004–2008 were analysed (n = 3069 collection events comprising 8755 species records). Only species with over 20 records were included. The records were mostly from specific site surveys, rather than general 1-km² surveys: 66.2 % of the surveys in which *H. axyridis* was one of the species were recorded at 100 m square resolution or higher. In order to reduce the potential bias caused by a small number of sites being surveyed many times on different dates, a grid reference was excluded from the dataset if the grid reference/date combination had more than 40 records. The British spatio-temporal index was calculated by dividing the number of records where *H. axyridis* was recorded with a certain species by the total number of records for that species with any other ladybird, including *H. axyridis*.

The three national co-occurrence indices were then used to assess the likelihood of encounter in three-point scales. Since sampling and calculation methods differed in the three countries, the range of the indices differed. Therefore, for each country, the index range (i.e. the range between the minimum and the maximum indexes) was divided into three sections of equal length and scored as follows: for species with index values in the highest section, the likelihood of encounter was considered very likely (score 3), for those in the mid section, moderately likely (score 2) and for those in the lowest section, unlikely (score 1):

3. Encounter very likely: Swiss data: above 46.4 %, Belgian data: above 57.0 %, British data: above 13.9 %
2. Encounter moderately likely: Swiss data: 23.3–46.4 % in, Belgian data: 38.7–57.0 %, British data: 8.7–13.9 %
1. Encounter unlikely: Swiss data: less than 23.3 %, Belgian data: less than 38.7 %, British data: less than 8.7 %

For each species, a final score of likelihood of encounter was given, corresponding to the average of the country scores, rounded to the nearest unit. Where only two countries provided a score for a particular species and these scores differed by one unit, the highest score was selected.

Competition for food

A three-point scale was adopted to assess the exposure to competition for food, progressing from minimal hazard (1) to major hazard (3). The exact degree of competition for food at the field-scale is extremely difficult to assess. Nevertheless, the most obvious determinant of whether competition for food represents a problem is whether the diet utilised by a given species is also utilised by *H. axyridis*. *Harmonia axyridis* is recognised as a primarily aphidophagous species, but is able to feed on other insects (Hodek and Evans 2012). Thus, aphidophagous species will be most exposed to competition for food with *H. axyridis*. Competition for coccids, adelgids or other insects is a possibility but probably less likely than competition for aphids. Finally, species utilising more unusual diets, such as mildew, pollen and plants will be least exposed to competition for food. Data on dietary requirements of European ladybirds was obtained

from the literature (e.g. Majerus 1994; Roy et al. 2011; Hodek and Evans 2012) and used to assign each species to one of the following score categories:

3. Major hazard: feeds principally on aphids
2. Moderate hazard: feeds principally on other insects
1. Minor hazard: feeds principally on non-insect food

Intra-guild predation (IGP)

The consequence of IGP between *H. axyridis* and native species was assessed through experimental data available for 14 out of the 30 native species. Defensive strategies against IGP at a range of life stages were also considered. Methods and results are described in detail in Ware et al. (2008a), Ware and Majerus (2008) and Katsanis et al. (2013). Similar studies from Félix and Soares (2004), Nóia et al. (2008) and Rondoni et al. (2012a, b) were also included in the assessment for two native species not covered by the three previously cited references, i.e. *Coccinella undecimpunctata* L. and *Platynaspis luteorubra* Goeze. To summarise, Petri-dish tests were conducted to collect data on: the susceptibility of different coccinellids at the egg stage to predation by first instar *H. axyridis* larvae, the susceptibility of coccinellids at the pre-pupal and pupal stage to predation by the last (fourth) instar *H. axyridis* larval stage, and the outcome of confrontation between *H. axyridis* and the larvae of native species at first or fourth instar larvae. In each case, single larvae were exposed to either single eggs, single larvae, pupae or pre-pupae for a period of 24 or 48 h, without the presence of any other food source. The full range of tests was carried out with *A. bipunctata*, *A. decempunctata* (L.), *Anatis ocellata* (L.), *Calvia quatuordecimguttata* (L.), *Coccinella septempunctata* L., *Harmonia quadripunctata* Pontoppidan, and *Propylea quatuordecimpunctata* (L.). Egg predation was not tested with *Coccinella quinquepunctata* L. and predation on pre-pupae and pupae was not tested on *Aphidecta oblitterata* (L.), *Calvia decemguttata* (L.), *Hippodamia variegata* (Goeze) and *Oenopia conglobata* (L.). Data on predation on fourth instar larvae on *P. luteorubra* were retrieved from Rondoni et al. (2012a, b) whereas Félix and Soares (2004) and Nóia et al. (2008) provided tests on all developmental stages of *C. undecimpunctata*.

The work described above in effect addressed physical and chemical defence only. In reality, a range of behavioural tactics may be employed to reduce the risk of predation, many of which may be unnoticeable within the confines of a Petri-dish. Certain behavioural strategies may provide effective immediate escape from the risk of IGP by *H. axyridis*, such as high mobility of larvae compared to *H. axyridis* and dropping off the plants when a predator approaches (Sato et al. 2005). Such defence strategies, when known from the literature or from unpublished observations, were taken into account in the assessment of the 14 tested species, as described below.

Based on the above, species were assigned to hazard scores as follows:

3. Major hazard: Native species highly susceptible, i.e. asymmetric IGP in favour of *H. axyridis* observed in at least two life stages, and no asymmetric IGP in favour of the native species observed in any stage, and short-term behavioural avoidance unlikely (i.e. no obvious strategies documented or observed for this species).
2. Moderate hazard: Native species less susceptible, i.e. no asymmetric IGP in favour of the native species observed in any stage but asymmetric IGP in favour of *H. axyridis* not observed in more than one life stage. Or, if IGP observed in more than one life stage, short-term behavioural avoidance observed and/or described in the literature.
1. Minor hazard: Asymmetric IGP in favour of the native species observed in at least one life stage, i.e. physical or chemical defences present at all or some life stages.

The 18 species that were not tested were given a moderate hazard score (2).

Final risk assessment

A total risk index score was calculated for each of the 30 native species, by multiplying the score of the likelihood of encounter by the sum of the two hazard scores. Ladybirds reaching the maximum risk index of 18 ($3 \times (3 + 3)$) were considered at very high risk, and those with scores of 12–15, 8–10 and 2–6 were considered at high, medium and low risk, respectively.

Results

Likelihood of encounter with *H. axyridis* in the field

Scores for likelihood of encounter were generally consistent in the three countries, particularly for those species with high scores (Table 1). The species with the highest co-occurrence indices, i.e. those most likely to encounter *H. axyridis* in the field, were aphidophagous species living principally on broadleaved trees, i.e. *Adalia* spp., *Calvia* spp. and *O. conglobata*. For example, in Switzerland, 69.8 % of the *A. bipunctata* adults were collected together with at least one *H. axyridis*. The lowest indices and scores were obtained by species living in grasses, in particular the pollen and fungus feeding *Tythaspis sedecimpunctata* (L.) or the phytophagous *Henosepilachna argus* (Geoffroy) or *Subcoccinella vigintiquatuorpunctata* (L.) (Table 1). No specimen of these three species was collected with *H. axyridis* during our surveys in Switzerland. Aphidophagous species associated with conifers, such as *A. oblitterata* and ubiquitous species such as *C. septempunctata* and *P. quatuordecimpunctata* scored low, particularly in Switzerland, where only 3.4, 2.3 and 20.5 % of the adults of these three species were collected with *H. axyridis*, respectively. In Britain and Belgium, *H. axyridis* co-occurred to a moderate extent with *C. septempunctata*, especially where nettles (*Urtica* spp.) were prominent. Also, overall there was a moderately high co-occurrence in Britain and Belgium with conifer specialists such as *H. quadripunctata*, *A. ocellata* and *Myrrha octodecimpunctata* (L.). Another conifer species, *Myzia oblongoguttata* (L.) even scored high in Britain although *H. axyridis* is not abundant on pine trees in at least parts of England (Brown et al. 2011).

Competition for food

From the 30 species included in the assessment, 19 are principally aphidophagous and were scored 3 to indicate the high potential for competition for food (Table 2). Chilocorinae (*Chilocorus* spp. and *Exochomus* spp.) feed mainly on scale insects. *Aphidecta oblitterata* is mainly a predator of Adelgidae and *Coccinella hieroglyphica* L. feeds mainly on Chrysomelidae. They received a score of 2. Finally, three phytophagous species (*Cynegetis impunctata*

(L.), *H. argus* and *S. vigintiquatuorpunctata*) and three mostly mycophagous species (*Halyzia sedecimguttata* (L.), *Psyllobora vigintiduopunctata* (L.) and *T. sedecimpunctata*) were scored 1.

Intra-guild predation (IGP)

Results of IGP tests are described in detail in previous publications (Félix and Soares 2004; Ware and Majerus 2008; Ware et al. 2008a; Rondoni et al. 2012a, b; Katsanis et al. 2013). From the 14 species in which IGP with *H. axyridis* was assessed, nine were highly vulnerable to IGP by *H. axyridis* and behavioural avoidance is not known. Thus these received a score of 3 (Table 2). Two of the tested species were scored 1. Eggs of *C. quatuordecimguttata* were avoided by *H. axyridis* larvae due to an external chemical deterrent (Ware et al. 2008b; Katsanis et al. 2013). Larvae of *C. quatuordecimguttata* were also less vulnerable to IGP than the other species tested and showed mostly symmetric IGP with *H. axyridis* larvae. *Anatis ocellata* larvae acted as the only asymmetric intra-guild predator of *H. axyridis* larvae (Katsanis et al. 2013). These results are attributed to differences in physical defensive structures: larvae of *H. axyridis*, *A. ocellata* and, to a lesser extent, *C. quatuordecimguttata* are protected by a covering of thick dorsal and dorsolateral spines, whereas larvae of other species possess fine hairs only, or are sometimes almost smooth (Ware and Majerus 2008; Roy et al. 2011). The only exception was *H. quadripunctata*, which has spiny larvae similar to those of *H. axyridis* but was asymmetrically vulnerable to *H. axyridis* in the fourth instar and pre-pupal stages (Ware and Majerus 2008). Three species that are also vulnerable to IGP by *H. axyridis* in Petri-dishes were nevertheless given a score of 2. *Propylea quatuordecimpunctata* larvae are noticeably long-legged and mobile and are, therefore, more able to escape attack in the field (R. Poland, unpublished data). In addition, larvae of *C. septempunctata* are commonly reported to drop from a host plant if a potential predator approaches (Sato et al. 2005; Raak-van den Berg et al. 2012). *Platynaspis luteorubra* was tested only in the fourth instar, by Rondoni et al. (2012a, b). Although the IGP was asymmetric in favour of *H. axyridis*, they noticed that *P. luteorubra* was not very susceptible to attack by *H. axyridis*, which exhibited lower rates of successful attack and predation on *P. luteorubra* than, e.g., *A. bipunctata*.

Table 2 Dietary specialisation and effective defensive strategies against *H. axyridis* of the 30 European coccinellids assessed in the study and ascribed competition and predation scores

Species	Principal food	Competition Score	Defensive strategies	Predation Score
<i>Adalia bipunctata</i>	Aphids	3	None	3
<i>Adalia decempunctata</i>	Aphids	3	None	3
<i>Anatis ocellata</i>	Aphids	3	Physical	1
<i>Anisosticta novemdecimpunctata</i> ^a	Aphids	3	Unknown	2
<i>Aphidecta oblitterata</i>	Adelgids	2	None	3
<i>Calvia decemguttata</i>	Aphids	3	None	3
<i>Calvia quatuordecimguttata</i>	Aphids	3	Physical, chemical	1
<i>Chilocorus bipustulatus</i> ^a	Coccids	2	Unknown	2
<i>Chilocorus renipustulatus</i> ^a	Coccids	2	Unknown	2
<i>Coccinella hieroglyphica</i> ^a	Chrysomelids, aphids	2	Unknown	2
<i>Coccinella magnifica</i> ^a	Aphids	3	Unknown	2
<i>Coccinella quinquepunctata</i>	Aphids	3	None	3
<i>Coccinella septempunctata</i>	Aphids	3	Behavioural	2
<i>Coccinella undecimpunctata</i>	Aphids	3	None	3
<i>Cynegetis impunctata</i> ^a	Plants	1	Unknown	2
<i>Coccinula quatuordecimpustulata</i> ^a	Aphids	3	Unknown	2
<i>Exochomus nigromaculatus</i> ^a	Coccids, adelgids and other woolly aphids	2	Unknown	2
<i>Exochomus quadripustulatus</i> ^a	Coccids	2	Unknown	2
<i>Halyzia sedecimguttata</i> ^a	Mildew	1	Unknown	2
<i>Harmonia quadripunctata</i>	Aphids	3	Physical	3
<i>Henosepilachna argus</i> ^a	Plants	1	Unknown	2
<i>Hippodamia variegata</i>	Aphids	3	None	3
<i>Myrrha octodecimguttata</i> ^a	Aphids	3	Unknown	2
<i>Myzia oblongoguttata</i> ^a	Aphids	3	Unknown	2
<i>Oenopia conglobata</i>	Aphids	3	None	3
<i>Platynaspis luteorubra</i>	Aphids	3	Poor	2
<i>Propylea quatuordecimpunctata</i>	Aphids	3	Behavioural (running)	2
<i>Psyllobora vigintiduopunctata</i> ^a	Mildew	1	Unknown	2
<i>Subcoccinella vigintiquatuorpunctata</i> ^a	Plants	1	Unknown	2
<i>Tytthaspis sedecimpunctata</i> ^a	Pollen, mildew, non-homopteran arthropods	1	Unknown	2

^a Species that were not experimentally assessed for the impact of intra-guild predation

Information on principal food was obtained from the literature (e.g. Majerus 1994; Roy et al. 2011; Hodek and Evans 2012). For defensive strategies, see the text

Final risk assessment

Four species, *A. bipunctata*, *A. decempunctata*, *C. decemguttata* and *O. conglobata* achieved the maximum possible risk score of 18. *Myzia oblongoguttata* was scored 15 and *C. quinquepunctata*, *C.*

undecimpunctata and *H. quadripunctata* were given a score of 12. These four species are therefore also considered as being at relatively high risk. Eleven species achieved a score of 8–10, suggesting a moderate risk, and 11 species reached a low risk score of 2–6 (Table 3).

Table 3 Final assessment of the risk posed to 30 European coccinellids by *Harmonia axyridis*

Species	Likelihood of encounter	Competition score	Predation score	Total risk score
Very high risk				
<i>Adalia bipunctata</i>	3	3	3	18
<i>Adalia decempunctata</i>	3	3	3	18
<i>Calvia decemguttata</i>	3	3	3	18
<i>Oenopia conglobata</i>	3	3	3	18
High risk				
<i>Myzia oblongoguttata</i> ^a	3	3	2	15
<i>Coccinella quinquepunctata</i>	2	3	3	12
<i>Coccinella undecimpunctata</i>	2	3	3	12
<i>Harmonia quadripunctata</i>	2	3	3	12
Medium risk				
<i>Anisosticta novemdecimpunctata</i> ^a	2	3	2	10
<i>Coccinella magnifica</i> ^a	2	3	2	10
<i>Coccinella septempunctata</i>	2	3	2	10
<i>Coccinula quatuordecimpunctata</i> ^a	2	3	2	10
<i>Myrrha octodecimguttata</i> ^a	2	3	2	10
<i>Platynaspis luteorubra</i>	2	3	2	10
<i>Anatis ocellata</i>	2	3	1	8
<i>Calvia quatuordecimguttata</i>	2	3	1	8
<i>Chilocorus bipustulatus</i> ^a	2	2	2	8
<i>Exochomus nigromaculatus</i> ^a	2	2	2	8
<i>Exochomus quadripustulatus</i> ^a	2	2	2	8
Low risk				
<i>Cynegetis impunctata</i> ^a	2	1	2	6
<i>Halysia sedecimguttata</i> ^a	2	1	2	6
<i>Hippodamia variegata</i>	1	3	3	6
<i>Aphidecta oblitterata</i>	1	2	3	5
<i>Propylea quatuordecimpunctata</i>	1	3	2	5
<i>Chilocorus renipustulatus</i> ^a	1	2	2	4
<i>Coccinella hieroglyphica</i> ^a	1	2	2	4
<i>Henosepilachna argus</i> ^a	1	1	2	3
<i>Psyllobora vigintiduopunctata</i> ^a	1	1	2	3
<i>Subcoccinella vigintiquatuorpunctata</i> ^a	1	1	2	3
<i>Tytthaspis sedecimpunctata</i> ^a	1	1	2	3

^a Species that were not experimentally assessed for the impact of intra-guild predation

See text for description of risk categories and scoring method

Discussion

The risk assessment method presented here allows us to rank European coccinellids according to their order of risk from negative interactions with *H. axyridis*, thus informing the direction and focus of conservation and control initiatives. The four species identified as

being most at risk, *A. bipunctata*, *A. decempunctata*, *C. decemguttata* and *O. conglobata*, are usually found on deciduous trees, where *H. axyridis* is also found most commonly. They are primarily aphidophagous and have immature stages which are highly vulnerable to IGP by *H. axyridis*. *Calvia quatuordecimguttata* is another aphidophagous species living on

broadleaved trees, and, thus, is likely to encounter and compete with *H. axyridis* in the field. However, in contrast to other European species, its eggs are protected by a chemical deterrent and its larvae are protected by strong spines, lowering the risk of displacement by *H. axyridis* (Ware et al. 2008b; Katsanis et al. 2013, 2016).

Phytophagous and mycophagous ladybird species are clearly at lower risk because they do not compete for the same resource and will be less likely to encounter *H. axyridis* than homopter-an-feeding ladybirds. Aphidophagous species found mainly or exclusively on conifers and in grasslands seem to be at medium risk. *Harmonia axyridis* shows a strong preference for broadleaved habitats compared to conifers and grasslands, as shown by our asymmetric habitat overlap index calculated in Switzerland. However, observations from Belgium show that it can also be a dominant species on conifers (Adriaens et al. 2008). It is also very abundant within herbaceous crops (e.g. Colunga-Garcia and Gage 1998; Jansen and Hautier 2008) but surveys in Switzerland and Britain showed that, more than ten years after its arrival, it is still an uncommon species in grasslands, except when specific plants, such as nettles, are present (Roy et al. 2011; Kenis, unpublished data).

Among the three risk components considered in the method, the assessment of the likelihood of encounter is a key element, albeit difficult to assess, particularly for uncommon species. We were fortunate that data from ladybird surveys were available from three countries over a relevant time period. However, these surveys were not carried out specifically for the purpose of risk assessment and, therefore, the data are not ideal for assessing habitat overlap. In particular, data from Belgium and, to a lesser extent, Britain, are available at relatively low spatial resolution, which may still contain different habitats, such as broadleaved trees and conifers or grasslands. Because of this scale issue, the likelihood of encounter of a species with *H. axyridis* could be over-estimated. However, the results are relatively consistent with a previous study showing high niche similarity between *H. axyridis* and these species at lower spatial scale, i.e. based on co-occurrence on the same plants (Adriaens et al. 2008). The common generalist species *C. septempunctata* appears to be stable in distribution and abundance across Europe, despite the arrival of *H. axyridis* (Roy et al. 2012). The defensive behavioural

strategy of its larvae may partly explain this. However, this species is mainly associated with herbaceous vegetation and low-scale spatio-temporal co-occurrence indices may overestimate the likelihood of encounter with *H. axyridis*. Swiss records were made at a higher spatial resolution, i.e. a specific meadow, a broadleaved hedge or a group of trees of a single conifer species. However, the Swiss dataset is smaller than the datasets from the two other countries and so less species could be properly assessed for their co-occurrence with *H. axyridis*. For example, *C. quinquepunctata* and *C. undecimpunctata*, found mainly on low vegetation, were not present in the Swiss dataset and it is possible that, for these two species, the likelihood of encounter based on the Belgian and British dataset (2) and, consequently, the final risk scores (15) were overestimated. Furthermore, all records in Switzerland and most of them in Britain and Belgium were of adult ladybirds, while co-occurrence of larvae would be especially relevant since immature life stages are more susceptible to IGP and competition for food than adults, which are more mobile (Pell et al. 2008). However, for a given ladybird species, the adults and larvae use the same feeding resources and tend to frequently co-occur (e.g. Brown et al. 2011). It could be argued that the likelihood of encounter could be derived from general habitat preference data gathered from the literature. However, such data are too vague for most native coccinellid species, and often inconsistent between information sources and geographic areas.

Effects of direct interactions and defensive mechanisms are straightforward to assess but the rearing of high numbers of ladybird species is time-consuming and some species are difficult to rear due to their specific diets. Therefore, these effects could only be assessed by the authors for 12 species and retrieved from other publications for two additional species. For the remaining 16 species, putative predation scores could be derived from defence mechanisms of taxonomically or morphologically related species. However, without specific IGP experiments, it would have been impossible to observe, e.g. that *C. quatuordecimguttata* eggs are chemically protected against predation while eggs of the closely-related *C. decemguttata* are not (Katsanis et al. 2016). Large larval spines, such as those of *H. axyridis*, *A. ocellata* and *C. quatuordecimguttata* seem to provide effective mechanical defence against IGP (Katsanis et al. 2013).

However, other spiny larvae such as those of *H. quadripunctata* are vulnerable to *H. axyridis* predation (Ware and Majerus 2008). Furthermore, unpublished observations (A. Katsanis) showed that *H. axyridis* larvae are able to avoid spiny larvae of *Exochomus quadripustulatus* (L.) by biting them at their softer ventral surface. Other experiments, using *H. axyridis* larvae in which spines had been removed by hand, showed that spines of *H. axyridis* allow reducing the bites from *C. septempunctata* but do not increase survival, suggesting that spines are not the major component of its defence (Hautier 2012). For these reasons, all non-tested species were given a medium predation score of 2 until proper experiments are made. It must be noted that, even if the non-tested species had been scored high (3) in IGP tests, only one of them, *M. oblongoguttata*, would present a final risk that is as high as that of the top four species because all the others showed a lower likelihood of encounter. It could also be argued that observation of IGP in a Petri-dish does not necessarily translate to occurrence in the field. Analyses of exogenous alkaloids or DNA in field-collected *H. axyridis* provide useful tools but will generally identify the most common species (Hautier et al. 2011; Thomas et al. 2013; Rondoni et al. 2014; Brown et al. 2015). Furthermore, the abundance of the extra-guild prey (e.g. aphids) may affect IGP (Nóia et al. 2008). Thus, when possible, extraguild prey should be included in IGP tests.

Dietary overlap is the best determinant we found for evaluating the level of hazard due to competition for food, although we realise that this parameter is linked to the likelihood of encounter, which depends on resource similarity, since eggs are laid close to resources (Majerus 1994). One way to improve the assessment would be to consider the ladybird diet more precisely, i.e. to prey species or genus level, but this requires a precise knowledge of ladybird diets and preferences, which, for the moment, is largely lacking (Hodek and Evans 2012). Competitive interaction studies on competition for food between *H. axyridis* and European ladybirds are rare. Soares and Serpa (2007) showed that the presence of *H. axyridis* adults significantly affected the reproductive capacity of *C. undecimpunctata* even when the resource was not in short supply.

It remains to be seen whether long-term studies on ladybird species abundance that are presently being carried out in the three countries will validate our risk

assessments. The Holarctic *A. bipunctata*, one of the species identified as most at risk in this study, has declined severely in the last 20 years in North America, possibly due to the invasion of *H. axyridis* and other exotic ladybirds (Harmon et al. 2007; Bahlai et al. 2015). Strong evidence of a decline of *A. bipunctata* and, to a lesser extent, other native species has been demonstrated in Britain, Belgium and Switzerland (Brown et al. 2011; Roy et al. 2012; Comont et al. 2014; Adriaens et al. 2015). In Belgium and Britain, *H. axyridis* has been shown to commonly feed on *Adalia* spp. in the field (Hautier et al. 2011; Thomas et al. 2013; Rondoni et al. 2014; Brown et al. 2015). Interestingly, *A. bipunctata*, the species that shows by far the strongest decline in Europe, is also the one that showed the highest likelihood of encounter with *H. axyridis* in our study, in particular in Switzerland where records were made at the highest spatial resolution. Had we based this assessment solely on the literature, we would probably have considered the congeneric *A. decempunctata* as having a higher likelihood of encountering *H. axyridis* than *A. bipunctata* because of its strong association with arboreal, broadleaved habitats. However, general long-term surveys, while suitable for assessing trends in abundant species, are less appropriate for detecting effects on rare species, which were sparsely recorded prior to the arrival of the invasive alien species. Therefore, it is essential that specific studies are conducted focusing on species found historically at lower abundance and which were also ascribed high scores in our risk assessment (such as *C. decempunctata*, *O. conglobata* and *C. quinquepunctata*). The relative scarcity of these species coupled with their restricted ecological niches could enhance the risk of local extinction.

Many generic assessment methods exist to assess the broad risk of invasive species, including predators, introduced accidentally or as biological control agents (e.g. van Lenteren et al. 2006; D'hondt et al. 2015; Kumschick et al. 2015). Other, more specific risk assessments focus on the hazard of predation on a single prey (e.g. Koch et al. 2006). However, the risk assessment method presented here is unique in the sense that it allows us to rank a whole set of native species, according to their order of risk from negative interactions with the invasive species. It is hoped that the risk assessment method proposed here could be applied to other situations where the arrival of an alien predator potentially threatens native species through

competition and intra-guild or extra-guild predation. Classifying competitor or prey species according to their exposure and vulnerability, and selecting the most vulnerable species for research, protection and conservation programmes could be a useful approach. Potential candidates include, among others, several invasive alien predatory wasps and hornets that threaten biodiversity worldwide. For example, the Asian hornet, *Vespa velutina*, a recent invader in Western Europe, may displace various native insects such as bees, flies and vespid wasps through direct predation and competition (Beggs et al. 2011). The same approach could also be considered for assessing the risk of invasive ants since these are also generalist predators that are known to threaten native species, in particular ants, through various mechanisms (Holway et al. 2002). Furthermore, this approach is not limited to insects. Other predatory terrestrial and aquatic invertebrates would be suitable for similar assessments. For example, the killer shrimp, *Dikerogammarus villosus*, has undergone an explosive invasion in Europe in the last two decades and has recently been found in Britain (MacNeil et al. 2010), where a similar risk assessment could be performed to evaluate which native gammarids or other aquatic invertebrates are most at risk. A similar protocol could be developed for invasive alien predaceous fish, amphibians, reptiles and even mammals, with some taxon-specific adaptations. The approach is primarily applicable to assess the risk posed to the displacement of native biodiversity by an invasive alien predator that is at an early stage of invasion, for which a firm impact cannot yet be ascertained but habitat and food overlaps can already be calculated. The approach should be used with more caution for risk assessments prior to invasion, but could for example complement pre-release risk assessment protocols for biological control agents (van Lenteren et al. 2006; Hajek et al. 2016), in which case a likelihood of encounter score could be estimated based on parameters such as general habitat requirements or feeding niches defined from data collected in the present distribution range of the species.

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